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The ant associates of Lycaenidae butterfly caterpillars – revisited

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Abstract. Based on a global compilation of data on ant associates of 523 Lycaenidae species, a synthesis is attempted as to which ants participate in these interactions. Ants from 63 genera have thus far been observed as visitors of facultative myrmecophiles or as hosts of obligate myrmecophiles among the Lycaenidae. Over 98% of records come from nectarivorous and trophobiotic ants in just three subfamilies, viz. Formicinae, Myrmicinae and Dolichoderinae, with the genera *Crematogaster* and *Camponotus* occupying the top ranks. Accumulation analysis suggests that rather few ant genera remain to be added to the list of associates. The representation of ant genera as attendants of lycaenid immatures is related to their global species richness, but with some notable exceptions. Ants that form ecologically dominant, large, long-lived colonies are over-represented as hosts of obligate myrmecophiles. The taxonomic diversity of lycaenid-ant associations is highest in the Oriental and Australian region, and lowest in the Neotropical and Afrotropical region. Among tropical African lycaenids, this is due to two butterfly lineages (genus *Lepidochrysops* and subfamily Aphnaeinae) that have massively radiated in the Neogene, but mostly maintaining their general affiliations with either *Camponotus* or *Crematogaster* ants, respectively. Many tropical and subtropical lycaenids nowadays form associations also with invasive alien tramp ants, giving rise to novel mutualistic interactions.

Introduction

The caterpillars of many species in the butterfly family Lycaenidae associate with ants (reviewed in: Fiedler 1991; Pierce et al. 2002). Multimodal communication between caterpillars and ants forms the mechanistic basis of these unusual associations (Fiedler et al. 1996; Casacci et al. 2019). With regard to their ecological outcome, these interactions cover the whole range from very loose non-aggressive occasional encounters, across facultative or obligate cases of mutualism, into rare cases of obligate social parasitism. In the latter, caterpillars enter ant nests to feed on ant brood or to beg trophallactic feeding. Along this continuum there occurs also a shift in the functional role of the ants. Whereas in facultative associations ants act as visitors of the caterpillars while these are feeding on their host plants, in cases of obligate mutualism or even social parasitism the ants serve as hosts for the butterflies. The identity and fidelity of ant visitors of facultative myrmecophiles obviously depends on the structure of the local ant community in each habitat and is thus quite unpredictable. Here the caterpillars, or also the female butterflies when selecting oviposition sites, have little control over which ant species will attend the larvae over their developmental period. As a consequence, facultative ant associations are usually unspecific, i.e. caterpillars of the same

lycaenid species may be visited by a more or less varied range of different ants. Host associations of obligate mutualists and parasites, in contrast, are far more specific. Either the mother butterfly establishes the association with appropriate hosts when selecting oviposition sites (ant-dependent oviposition: Pierce et al. 2002), or the caterpillars later on need to be actively adopted by proper host ants for completing their life cycle, as is the case with butterflies in the famous *Phengaris* (*Maculinea*) clade (Hayes 2015).

Out of the huge diversity of ants on Earth, only a fraction qualifies to act as potential partners in associations with lycaenid immatures. Three intertwined aspects of ant ecology are particularly relevant in that regard: nectarivorous feeding habits (Blüthgen and Feldhaar 2010), trophobiosis (Ness et al. 2010), and trophallaxis (Meurville and LeBoeuf 2021). Only ants that form mutualistic associations with honeydew-producing insects or with nectar-secreting plants and which share all the anatomical, physiological and behavioural characters essential for harvesting and sharing nutritive liquids are also able to attend lycaenid caterpillars.

Twenty years ago, I reviewed which ants participate in these interactions (Fiedler 2001). It turned out that out of the large array of ants that fulfil the aforementioned characters, ecologically prevalent taxa like *Crematogaster* and *Camponotus* by far dominate among ant visitors or hosts, but with characteristic variation between facultative and obligate interactions, or between biogeographical regions. Since that last attempt of a global synthesis, many new observations have been recorded. In particular, with the rise of the internet many pieces of information have now become accessible that remained elusive two decades ago. I therefore here set out to revisit the identity of ant associates of lycaenid butterflies. In particular, I will address the following research questions:

- How much has our understanding grown over the last 20 years? How complete is the coverage of ants attending lycaenid immatures in the meantime?
- Is the importance of ant taxa as associates of lycaenid immatures related to their global species richness?
- Is the visitor range of facultatively myrmecophilous caterpillars wider than the host ant range of obligate myrmecophiles?
- Are ant associations consistently more diverse in tropical rather than temperate regions?

Material and methods

Data collection

Starting from the data base underlying my earlier paper (Fiedler 2001), I continued to systematically collect journal articles that report on lycaenid-ant interactions. I also went through multiple faunal monographs in search of such records. Using Google Scholar, I searched for additional published records using search strings like *lycaenid ants attend*, *lycaenid ants associate*, or *lycaenid ants visit*. I also systematically (species by species) went through well curated and reliable web sites such as lepiforum.org (2021; Europe), butterflycircle.blogspot.com (Singapore), or Kunte et al. (2021) (India). Finally, I searched the pertinent web project "Ant-Butterfly Interactions" (Kaminski 2021) for additional records. The aim of this procedure was to obtain a data base as comprehensive as possible.

I only considered records of ant associations that were taken in the field. Observations from confrontations under laboratory or rearing conditions were disregarded. While essential to better

understand mechanistically the communication processes between caterpillars and ants, the focus of the present study is on interactions that form in nature. I also restricted my analyses to records where the involved ants had been identified at least to genus level, or where it was possible for me to post-hoc infer ant identity at genus level from accompanying photographs. Unfortunately, even in some rather recent and otherwise very detailed publications on lycaenid life-histories the identity of attendant ants was not assessed by ant taxonomists, and reports remain vague accordingly (e.g. van der Poorten and van der Poorten 2013).

Within the Lycaenidae, I excluded species in the subfamilies Poritiinae and Miletinae sensu Espeland et al. (2018). While in certain African representatives of the Poritiinae caterpillars occur exclusively on trees dominated by large colonies of *Crematogaster* ants (e.g. Sáfián and Larsen 2009; Sáfián and Collins 2014), these hairy larvae never possess nectar glands and therefore no trophobiosis with ants can take place in these cases. These caterpillars, which feed on lichens or algae growing on bark of ant trees, are functionally best described as commensalic to the *Crematogaster* ants which occupy the host trees. Larvae of most Miletinae are predators of honeydew-producing insects such as coccids, aphids or membracids, with a few species having evolved into social parasites of specific ants (Maschwitz et al. 1988; Lohman and Samarita 2009; Kaliszewska et al. 2015). Like in Poritiinae, Miletinae caterpillars have no nectar glands and in most cases ant associations they encounter are regulated by the trophobiotic interactions of their homopteran prey. I therefore decided to omit these (few) species from the analyses below, which also was the case in the 2001 study and thereby facilitates direct comparisons.

From this data base, I extracted record pairs of (butterfly species × ant genus). I used the ant genus (rather than species) as level of analysis for the following reasons. (1) Nectarivorous ants can rather readily be identified to genus level, even by non-specialists. In contrast, even in well documented faunas species-level identification of ants regularly requires access to special literature and to high-quality microscopy and biometry (for Europe: Seifert 2018). Both these resources are not available to most lepidopterists when encountering caterpillar-ant associations. (2) Unresolved cryptic species diversity is prevalent among ants. Even putatively well-known ant "species" like *Lasius niger* and *Lasius alienus* in Europe turned out to represent species complexes (Seifert 1991; Seifert and Galkowski 2016). Therefore, ant species-level "identifications" that have not been scrutinized by myrmecologists, or that can be retrieved only from older literature, are suspect. In contrast, generic affiliations of most ants have remained quite stable (see discussion below for a few exceptional cases relevant to visitors of lycaenid lavae). (3) Ant generic identities can often be inferred from photographic records, but species-level identifications are impossible in most such cases.

Within each butterfly species, I aggregated all association records with multiple species from the same ant genus into one record pair. For example, if one butterfly species was recorded as being visited by five different *Lasius* species, or if five sources mentioned associations with "*Lasius niger*", this was condensed into one single entry for '*Lasius*'. This procedure aimed at avoiding inflated representation of certain easily recognizable ants, or inflated records for butterfly species whose caterpillars are frequently found by lepidopterists. This approach also circumvents possible multiple counting of the same association, but under different ant species names. For example, in an old reference a caterpillar may have been reported as being attended by "*Lasius niger*", yet in a later paper exactly the same association might have been corrected to "*Lasius platythorax*". These ambiguities vanish at the ant genus level.

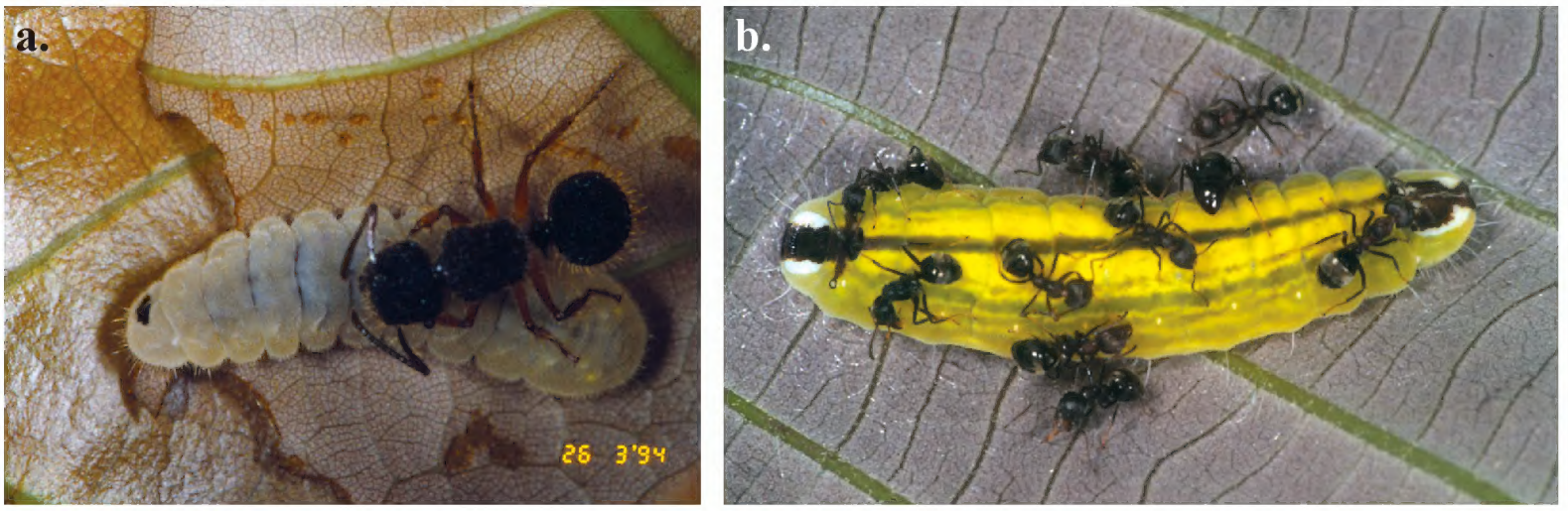

Figure 1. Exemplar species of (**a.**) a facultative myrmecophile (*Jamides virgulatus* attended by *Echinopla* sp.; left) and (**b.**) an obligate myrmecophile (*Flos anniella* attended by *Dolichoderus* sp., right) amongst the Lycaenidae. Observations from Poring, Sabah, Malaysia. Photo author K. Fiedler.

Data scoring

For each butterfly species, I scored whether its ant association is facultative or obligate (Fig. 1). Butterflies were scored as obligate myrmecophiles if their early stages are (almost) continually accompanied by ants, often with larger numbers of worker ants around, and especially if the females are known to oviposit only in the presence of their host ants. Ant-parasitic nest-inquiline lycaenid species were also classified as obligate myrmecophiles. All other butterfly species with ant associations were categorized as facultative myrmecophiles. I also noted whether the butterfly species occurs in one of the following biogeographical regions: Nearctic, Neotropical, Afrotropical (Africa south of the Sahara, including Madagascar), Palaearctic, Oriental (S and SE Asia, including the Indo-Malayan archipelago), or Australian (Australia, New Guinea and surrounding islands). In the few cases where butterfly species occur in more than one faunal region, the ant association records were allocated to the region where the pertinent observations had been made. This procedure avoids considering ant genera that may attend the caterpillars in one biogeographical region, but which do not occur in the other such region. For each ant genus observed, the global number of described species according to current taxonomy was extracted from the database AntWeb (2021).

Statistical analysis

The coverage of ant genera recorded in association with lycaenid caterpillars was assessed through the iNext Online software tool (Chao et al. 2016). Correlation analyses and calculation of diversity metrics were done using the package PAST 4.07 (Hammer et al. 2001).

Results

Global patterns of ant associates

The current compilation comprises data on ant associates of 523 lycaenid species (see Suppl. material 1: Appendix S1 for records and Suppl. material 2: Appendix S2 for the evaluated data sources). Ants from 63 genera in the seven subfamilies Dolichoderinae, Ectatomminae, Formicinae, Myrmicinae, Myrmeciinae, Ponerinae, and Pseudomyrmecinae have been observed to participate in these interactions (Fig. 2). This is an increase by 10 genera relative to the earlier

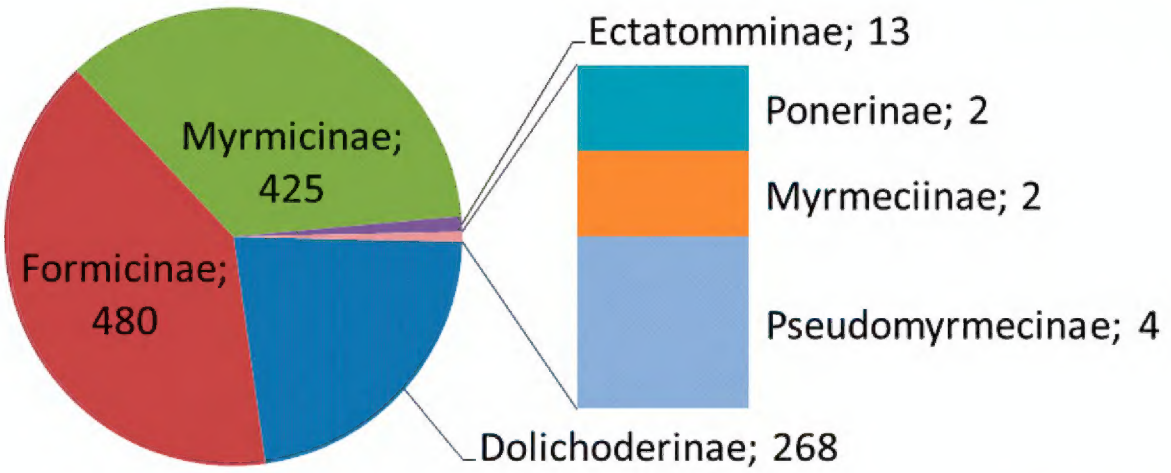

Figure 2. Representation of trophobiotic ant subfamilies in myrmecophilous associations of lycaenid butterflies. Figures indicate numbers of (butterfly species × ant genus) record pairs.

analysis. Altogether, 1194 record pairs are now available, compared to 817 data points in 2001, i.e. a substantial increase (by 46.1%) in the amount of observations. Collectively, observations with ants in the subfamilies Dolichoderinae, Formicinae and Myrmicinae account for 98.2% of all record pairs. The 10 globally most important ant genera as associates of lycaenid butterflies are (in descending order): *Crematogaster* (221), *Camponotus* (145), *Lasius* (66), *Tapinoma* (64), *Formica* (62), *Pheidole* (60), *Technomyrmex* (40), *Iridomyrmex* (36), *Plagiolepis* (33), and *Polyrhachis* (33). Most ant genera newly recorded since 2001 are known to attend larvae of just 1–3 lycaenid species and thus play only a very minor role. Two exceptions are related to shifts in the taxonomic circumscription of ant genera. Ant species now allocated to *Nylanderia* (recorded with 8 lycaenid species) were formerly included in *Paratrechina* (LaPolla et al. 2010). And the monobasic taxon *Iberoformica* (associated with 9 species) was only recently accepted as a distinct genus (Gómez et al. 2018). In contrast, '*Rhoptromyrmex*' was formerly viewed as a distinct genus, but has been downgraded into synonymy with *Tetramorium* (Ward et al. 2015).

Twelve ant genera have experienced a particularly strong increase (more than 10 additional record pairs) in their representation in the list of visitor or host ants. These are, in decreasing order: *Camponotus* (+55 spp.), *Crematogaster* (+43), *Tapinoma* (+23), *Technomyrmex* (+22), *Formica* (+22), *Plagiolepis* (+21), *Lasius* (+20), *Pheidole* (+19), *Monomorium* (+15), *Tetramorium* (+14), *Polyrhachis* (+13), and *Anoplolepis* (+11). All these had already earlier been well represented in the list of ant associates. Overall, the representation of ant genera in the list of associates was highly correlated across the data sets of the two points in time ($r = 0.986$, $p < 0.0001$; Fig. 3). *Camponotus* received disproportionally more new records than *Crematogaster*.

Overall, the documented diversity of ant associates, with 63 genera in 2021, appears slightly higher than the 53 genera reported 20 years ago (Fig. 4). A combined rarefaction-extrapolation analysis revealed a very high coverage of 0.9890 for 2001, and even 0.9899 for 2021. Even if extrapolating to over 1600 record pairs, the number of expected ant genera would only increase to about 66 (95% confidence interval: 60–73 ant genera).

The global species richness of the observed ant genera was positively related to their representation in the list of ant visitors and hosts ($r = 0.589$; $p < 0.001$), but with remarkable scatter (Fig. 5). Ants of the genus *Pheidole*, the by far most speciose ant genus on Earth, remain relatively under-represented as associates of lycaenid butterflies. The same is true for *Polyrhachis* (a highly

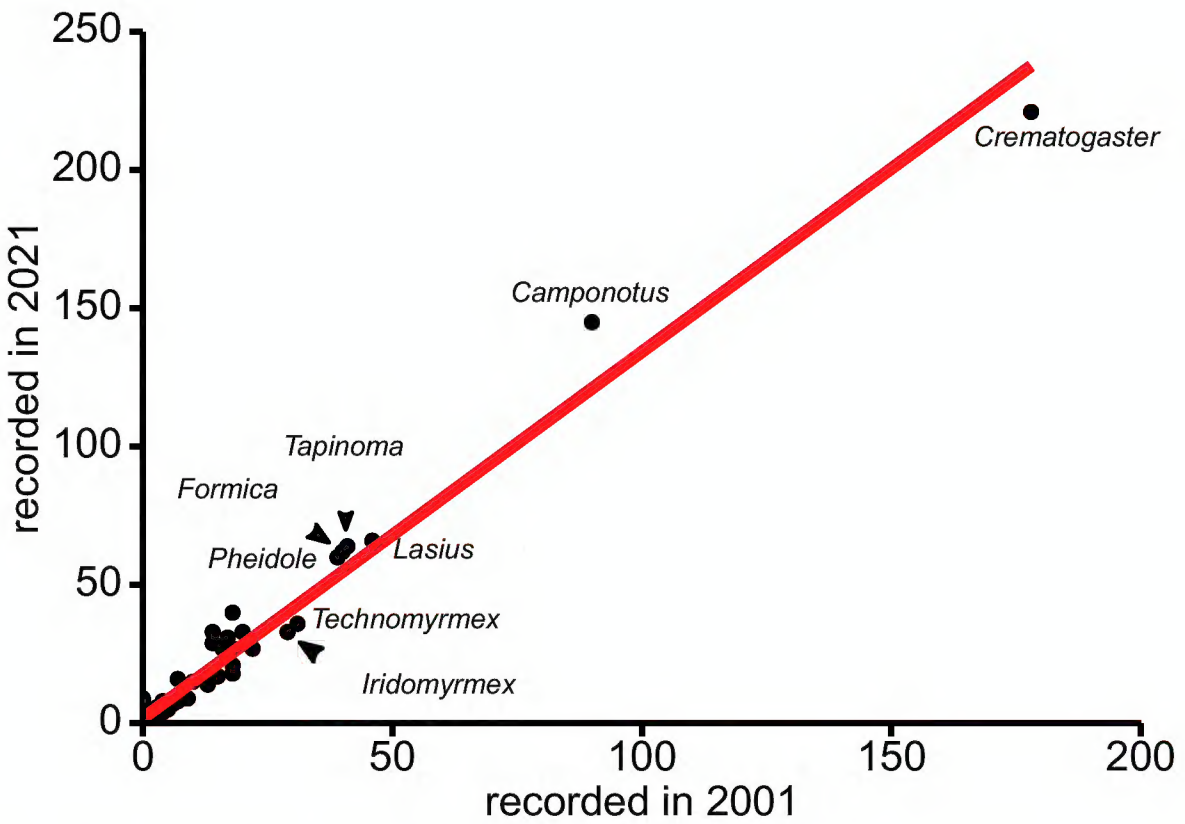

Figure 3. Representation of ant genera in the list of visitors or hosts of lycaenid caterpillars, comparing the 2021 with the 2001 data set. Each dot represents one ant genus. An ordinary least squares (OLS) regression line is fitted into the data cloud for visual clarity.

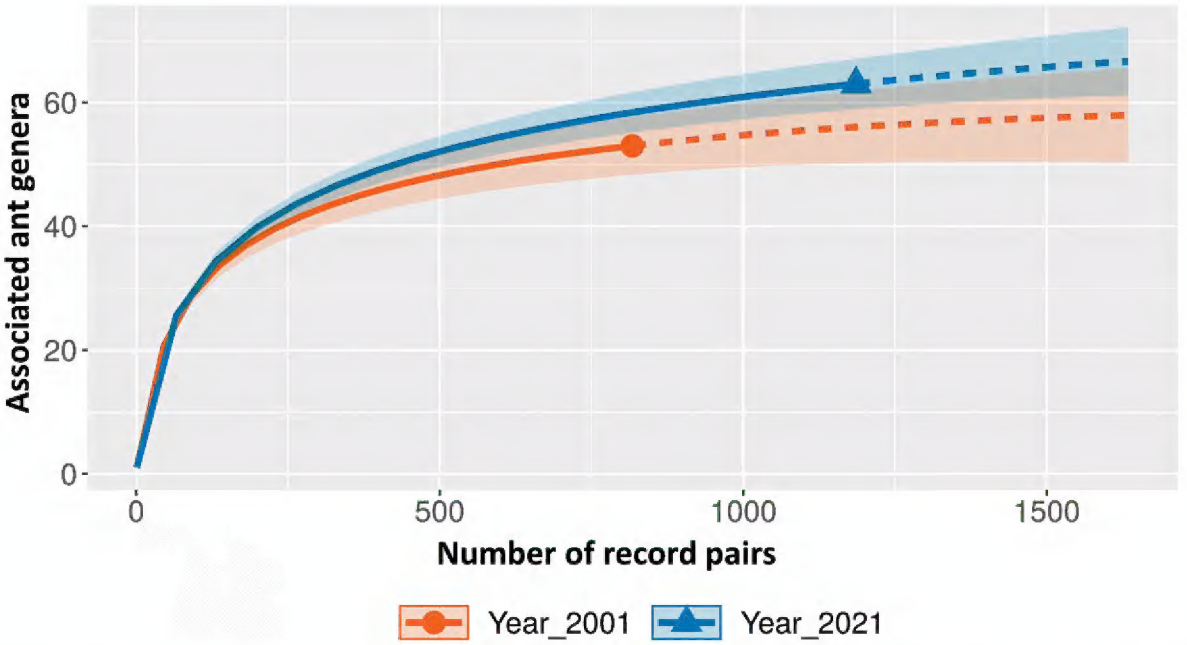

Figure 4. Rarefaction-extrapolation curves for the ant genera recorded as visitors or hosts of lycaenid caterpillars, comparing the data collections from 2001 and 2021, in relation to sampling success. Solid lines: rarefaction; dashed lines: extrapolation. Symbols denote observed level of records in either year.

trophobiotic ant genus of the Old World tropics), *Tetramorium*, and *Temnothorax*, even though all these ant genera experienced a substantial increase in record numbers (see above). In contrast, ants of the genus *Crematogaster* are distinctly over-represented relative to their global species richness. To a lesser extent, this also applies to *Formica*, *Lasius* and *Tapinoma*. Two extreme cases of deviance are the weaver ants *Oecophylla* (only 3 species recognized, but recorded from 27 lycaenid species) and *Anoplolepis* (9 species, yet also recorded with 27 lycaenid species).

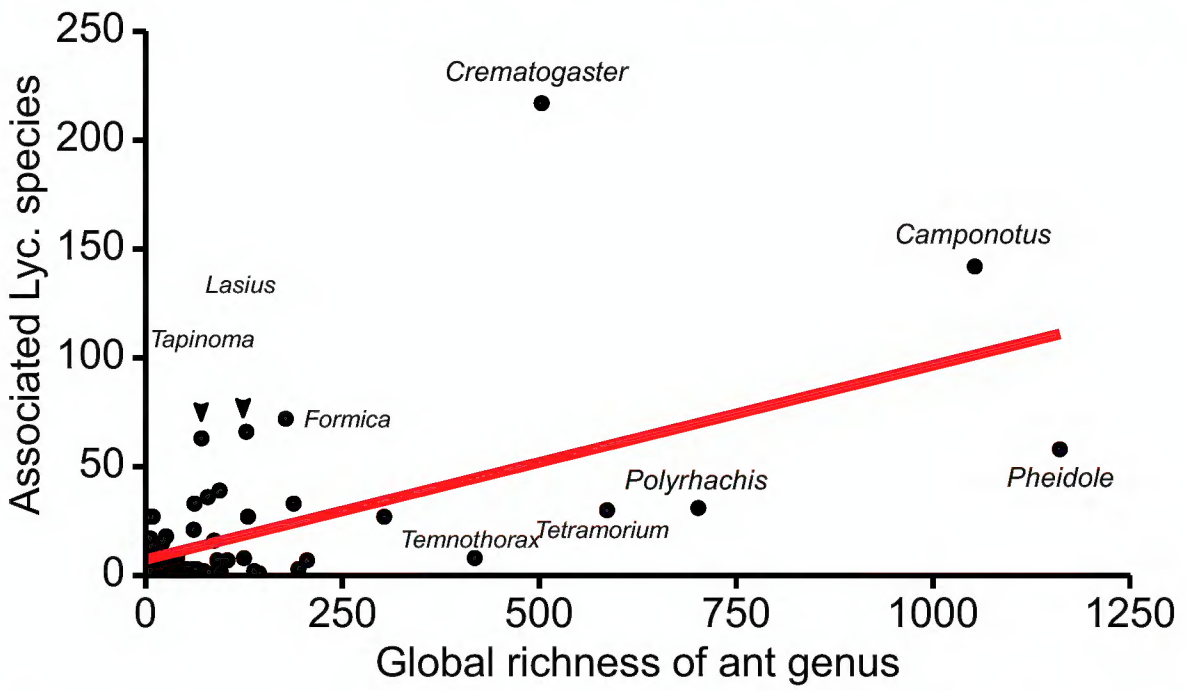

Figure 5. Representation of ant genera as hosts and visitors of lycaenid caterpillars, in relation to their global species richness. Each dot represents one ant genus. An OLS regression line is fitted into the data cloud for visual clarity. Ant genera below the regression line are under-represented, while those above the regression line are over-represented in relation to their global species diversity.

Obligate versus facultative myrmecophiles

Obligate myrmecophiles made up a considerable fraction in the data base (210 of 523 lycaenid species; 40.1%). As expected, the breadth of ant visitor ranges (Fig. 6) per butterfly species was far larger in facultative myrmecophiles than the breadth of host ant ranges among obligate myrmecophiles (Welch test, $t = 12.19$; $p < 0.0001$). Apart from a few exceptional 'aberrant' visitors that have been reported under unusual circumstances, obligate myrmecophiles are essentially affiliated with ant species within just one single genus each. In contrast, facultatively myrmecophilous caterpillars are visited by a much broader diversity of ants, reflecting the variation and unpredictability in local ant community composition and the number of records available per species from different studies. Thus far, larvae of 10 facultatively myrmecophilous lycaenid species have been observed being visited by ants from 10 or more genera: *Lampides boeticus* (15), *Ogyris oroetes* (13), *Plebejus melissa* (12), *Icaricia icarioides* (11), *Theclinesthes albocincta* (11), *Ogyris amaryllis* (10), *Jamides celeno* (10), *Echinargus isola* (10), *Nacaduba berenice* (10), and *Glaucopsyche lygdamus* (10).

Ant genera with stronger representation as visitors of facultative myrmecophiles also tended to serve as hosts for a larger number of obligate myrmecophiles ($r = 0.661$; $p < 0.0001$; Fig. 7). Four ant genera stand out as over-represented in this comparison: *Crematogaster*, *Oecophylla*, *Anonychomyrma*, and *Iridomyrmex*. In contrast, obligate associations with *Camponotus* ants appear to be slightly less numerous than one might expect from their strong representation in the visitors list at facultative myrmecophiles.

Diversity of lycaenid-ant associations

Contrary to expectation, the diversity of ant associations was not consistently highest in tropical realms. Rather, recorded associations in the Neotropical and Afrotropical regions showed lowest diversity, whereas ant partner diversity was highest among lycaenid butterflies from the Oriental and especially the Australian region (Fig. 8a). Ant interactions amongst Afrotropical lycaenids

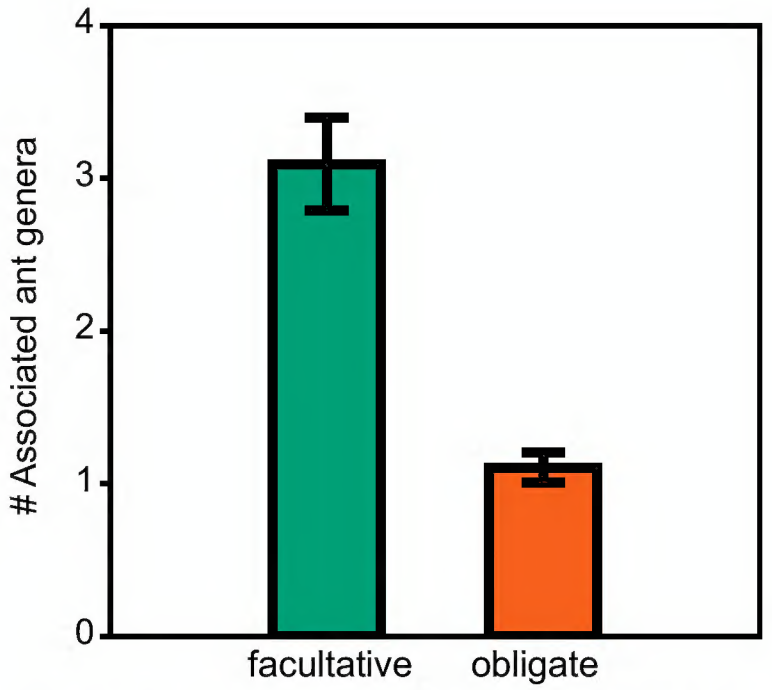

Figure 6. Mean number of genera of attendant ants that have been observed as visitors of facultative or as hosts of obligate myrmecophiles per Lycaenidae species. Error bars are 95% confidence intervals based on 9999 bootstrap randomizations.

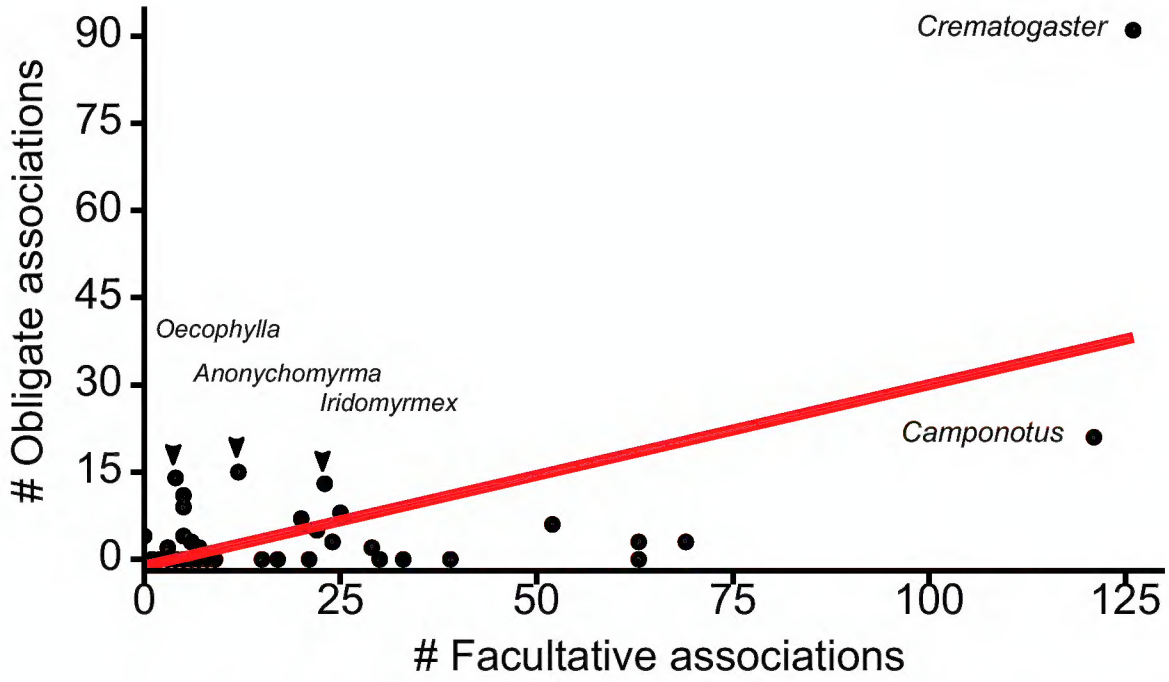

Figure 7. Representation of ant genera as hosts of obligately myrmecophilous lycaenid caterpillars, in relation to their frequency as visitors of facultative myrmecophiles. Each dot represents one ant genus. An OLS regression line is fitted into the data cloud for visual clarity. Ant genera below the regression line are under-represented, while those above the regression line are over-represented.

revealed the strongest dominance of one single ant genus, viz. *Crematogaster* in that case, accounting for almost half of all record pairs. In all other regions, the most prevalent ant genus accounted for only 15–25% of all available record pairs (Fig. 8b). *Crematogaster* ants were also the dominant visitors or hosts in the Oriental region (50 cases). This role was taken by *Iridomyrmex* in the Australian region (35), and by *Formica* in the Nearctic (26). In the Neotropical and Palaearctic region, *Camponotus* ants were most frequently recorded at caterpillars (with 16 and 56 lycaenid species, respectively).

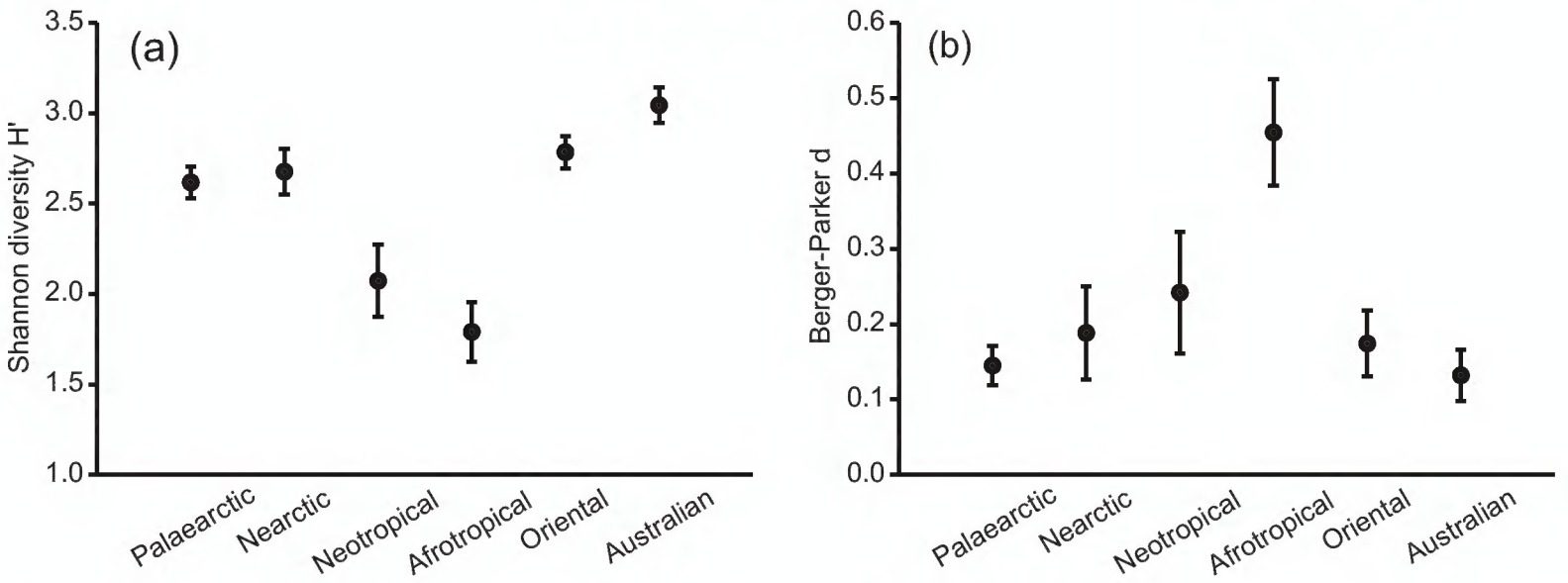

Figure 8. Diversity (**a.** measured as Shannon's H' metric) and dominance (**b.** expressed as Berger-Parker's d index) of recorded ant associations of Lycaenidae caterpillars across six biogeographical regions. Error bars denote 95% confidence intervals based on 9999 bootstrap replicates.

Discussion

Even though documentations of butterfly-ant interactions have substantially increased over the past 20 years, the global systematic, ecological, and biogeographical patterns to be recognized have turned out remarkably robust. Extrapolation analysis based on sample coverage suggests that further ant genera await discovery as visitors or hosts of lycaenid butterfly caterpillars, especially from still under-explored regions such as South America or tropical Africa. Yet, even a massive increase in records will likely just moderately augment the list of attendant ant genera. As expected, all recorded ant visitors and hosts belong to nectarivore or omnivore ant clades that frequently engage in trophobiosis with honeydew producing insects or in mutualism with plants bearing extrafloral nectaries. Based on signatures of stable C and N isotopes, many of these ants show a tendency towards "herbivorous" lifestyles, i.e. they are predacious on other insects only to a limited extent (Blüthgen et al. 2003; Feldhaar et al. 2010; Quinby et al. 2020).

Ants from just three subfamilies (Formicinae, Myrmicinae and Dolichoderinae) make up the vast majority (>98%) of recorded butterfly-ant associations. Within these subfamilies, only few genera are disproportionately represented. Globally, *Crematogaster* and *Camponotus* ants retain the top ranks. One important driver of that pattern are species-rich radiations of a few butterfly clades that maintain obligate, and in part parasitic, relationships with exactly these ants. Notable examples include the ant-parasitic genus *Lepidochrysops* in Africa (Espeland et al. in press) and the subfamily Aphnaeinae. The latter clade, with about 250 species distributed in Africa and southern to eastern Asia, shows strong co-evolution with its host ants, including multiple shifts to social parasitism and aphytophagy (Heath 1997; Boyle et al. 2015; Talavera et al. 2020), but in many cases bound to *Crematogaster* ants.

These features are also responsible for the strikingly low diversity of, and high dominance among, ant associations in the Afrotropical realm, where the preponderance of *Crematogaster* becomes most pronounced. If one were to include also the African Poritiinae into a similar analysis, the prevalence of *Crematogaster* would even increase further, since most species in the lichen-feeding tribes Liptenini and Epitolini appear to be associated with arboreal *Crematogaster* ant colonies (Larsen 2005).

Diversity of reported ant associations remained strikingly low for the Neotropical Lycaenidae species. Collectively, four arguments can be brought forward to explain that pattern. First, the life histories of South American lycaenids remain very incompletely documented, despite much research efforts in recent years, especially in Brazil (e.g. Bächtold et al. 2017 and references therein). Hence, a recording bias for sure still persists. Second, in the Neotropical region myrmecophilous caterpillars of many Riodinidae species occupy part of the ecological opportunities that elsewhere are exclusively held by lycaenids. Indeed, phylogenetic evidence suggests that not only myrmecophily in the Riodinidae evolved independently from the analogous associations in the Lycaenidae, but also that within the Riodinidae ant-associations evolved at least twice (Espeland et al. 2018). Recently, even parallel evolution of social parasitism with ants has been discovered among Neotropical Riodinidae (Kaminski et al. 2021). Therefore, various evolutionary options for myrmecophilous lycaenids might be pre-occupied by potentially competing riodinids. Third, most South American lycaenids belong to one single, though highly species-rich clade, namely the tribe Eumaeini (Robbins and Lamas 2004). In this tribe, caterpillars usually possess only a reduced set of ant organs (viz. they lack a pair of eversible tentacle organs, and in many species also the dorsal nectar gland is reduced). Fourth, ant assemblages in many Neotropical habitats are strongly dominated by two ant groups that never maintain trophobiotic associations with any other insects, viz. leafcutter ants and army ants (Hölldobler and Wilson 2010; Kronauer 2020). The frequent ecological dominance of these ants might further constrain the establishment of caterpillar-ant associations. Against this background, I hypothesise that even with much improved coverage of life-histories of Neotropical lycaenids the diversity of their ant associations will remain lower than in the Oriental or Australian faunal region. Nevertheless, South America is the most likely continent for the discovery of novel ant genera participating in caterpillar-ant interactions. For example, I predict that highly nectar-dependent *Cephalotes* ants (Hu et al. 2018; currently not recorded with any lycaenid species) will finally show up in the list of ant visitors at lycaenid larvae, as well as representatives of other omnivore or nectarivore genera like *Azteca* (thus far recorded only twice as visitors of lycaenids; see Brandão et al. (2012) for the functional diversity of Neotropical ants).

Some patterns in these associations may still be influenced by recording biases. For example, the over-representation of Holarctic ant genera like *Lasius* and *Formica* mirrors the ecological prevalence of these ants in northern temperate woodland and grassland biomes. Thus, for lepidopterists in Europe, Japan and North America these ants are the most likely visitors to be encountered when searching for lycaenid caterpillars in the field. However, many records published during the past two decades from the Mediterranean area (e.g. Lafranchis et al. 2007; Obregón-Romero and Gil-T. 2011; Obregón et al. 2015; Galanos 2020) have contributed to levelling out that bias and brought forward a much broader coverage of ant visitors at European lycaenid caterpillars.

On the other hand, especially in the Old World tropics a few ant genera remain under-represented. *Polyrhachis* ants, for example, are often highly trophobiotic, as also revealed by their isotopic signatures (Blüthgen et al. 2003). While additional associations between caterpillars and *Polyrhachis* ants have been recorded over the past two decades, they still lag behind what one might expect from their global species richness. Because *Polyrhachis* ants are usually arboreal, and often thrive in the canopy of tropical forests, the rather low representation of these ants might indicate a lack of coverage of lycaenid life-histories in that particular ecosystem. Insects of tropical tree crowns generally remain under-studied, and this also pertains to biota associated with social insects (Pérez-Lachaud and Lachaud 2014).

Facultative caterpillar-ant associations are essentially opportunistic and unpredictable. Those nectarivorous ants that dominate in a given ecosystem are also the most likely to be observed attending caterpillars, with further partitioning between ant species due to microhabitat preferences, times of day, and actual population densities. In contrast, more predictable patterns emerged among obligate myrmecophiles – with substantial parallels to host ant use among the rather few socially parasitic lycaenid clades (Fiedler 2012). Ecologically dominant ant species that form large and long-lived colonies are particularly rewarding hosts. These ants also harbour the largest arrays of myrmecophiles when it comes to nest inquilines (Parmentier et al. 2014; Parker 2016). This explains well the over-representation of rather species-poor, but highly dominant ants like *Oecophylla*, *Anonychomyrma*, or *Iridomyrmex*.

In recent years, invasive alien species have attracted ever more interest by ecologists, conservationists and evolutionary biologists alike (Kenis et al. 2009). Some of the most influential 'neobiota' are ants. For example, among the 100 'worst invasive species' identified by the IUCN (Lowe et al. 2000) five ant species are listed, three of which (*Linepithema humile*, *Anoplolepis gracilipes* and *Pheidole megacephala*) are well represented as visitors of lycaenid caterpillars. Indeed, the strong increase in records of *Anoplolepis* as attendants of lycaenid caterpillars is entirely due to many new associations observed in tropical countries like India, Singapore, Indonesia or Australia. Other invasive 'tramp' ants (McGlynn 1999) frequently observed as attending lycaenid caterpillars include *Technomyrmex 'albipes'*, *Tapinoma melanocephalum*, *Nylanderia bourbonica*, *Ochetellus glaber*, and *Paratrechina longicornis*. It has been commonly observed that invasive ants establish as efficient partners in generalized mutualistic interactions with other arthropods, while disruptions of mutualisms have often been reported in specific and highly co-evolved systems (Ness and Bronstein 2004; Toby Kiers et al. 2010). Very recently, also the reverse phenomenon has been recorded for the first time in butterfly-ant interactions: native *Lasius neoniger* ants in North America now attend caterpillars of an invasive lycaenid species, the European *Polyommatus icarus* that has become established in parts of the United States and Canada (Dexheimer et al. 2021).

In conclusion, the striking associations between lycaenid butterflies and ants continue to provide a fascinating topic from ecological as well as evolutionary perspectives. While we have arrived at a robust understanding of which ants, where, and why participate in these interactions, many facets await discovery, especially when it comes to elucidating hitherto completely unknown life histories. Still, for the majority of lycaenid species the intensity of their ant association remains insufficiently known and the identity of their interaction partners undisclosed. The present analysis, which would have been impossible without the recording efforts of many lepidopterists and citizen scientists around the world, therefore, is not only an attempt of a synthesis twenty years after a first such endeavour. It also aims at stimulating and inspiring colleagues to continue with "descriptive natural history" in the Anthropocene era of biodiversity loss and biotic homogenization.

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Supplementary material 1

Appendix S1

Authors: Konrad Fiedler

Data type: excel table.

Explanation note: Compilation of ant visitors or hosts recorded at 523 Lycaenidae species, where the taxonomic identity of ants has been documented at genus or species level. For each butterfly species its occurrence in gross biogeographical regions is also noted as a binary variable. In another column it is given whether the ant association is considered obligate (1) or not (0). The 10th column summarizes the number of ant genera involved in recorded interactions with each lycaenid species. The prefinal column contains the ant visitors or hosts, as they have been identified in the sources considered. It was impossible to validate whether all species level identifications are correct in view of current ant taxonomy. The final column gives the sources from which data on the identity of ant visitors or hosts were extracted. For a full bibliography see Suppl. material 2: Appendix S2.

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Link: https://doi.org/10.3897/nl.44.68993.suppl1

Supplementary material 2

Appendix S2

Authors: Konrad Fiedler

Data type: pdf-file.

Explanation note: List of published references (journal articles, book chapters and books) used to compile the list of ant visitors or hosts at 523 species of Lycaenidae butterflies.

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